

THE DISTRIBUTION OF THE SPECIES OF THE GENUS *PIERIS* IN NORTH AMERICA¹

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THE NORTH AMERICAN SPECIES of the Genus *Pieris* are distributed from the Arctic Ocean to Guatemala. However, none of the species of the genus (sensu stricto) exist in habitats which would be considered as tundra or arctic-alpine on the one hand, or as wholly tropical on the other. To this extent, the genus compares somewhat with *Colias*; the latter, however, contains two species that do exist in the tundra habitat.

The concept of a species which has been applied here is the same as that which has been applied previously to the species of the genus *Colias* in drawing the distribution maps for that genus (Hovanitz, 1950). This concept is based upon the consideration that the most important factor in stability of a species is the genetical population — or the interbreeding unit. Since, however, genes and their combinations cannot be seen, nor analyzed except by means of their effects on the appearance and physiology of the individuals carrying them, they must be studied through a comparative study of their morphological, anatomical or physiological characteristics. Thus, a name applied to one population may be applied to another population, or to many populations, if their characteristics indicate that a similarity exists between the hereditary makeup of such different populations. Such a name may cover quite a diversity of differences in the same population, or even a diversity of different populations if they are genetically separated one from the other by geographical or ecological means. The extent of gene interchange as well as the evaluation of the isolation mechanism determines whether or not one population should be considered as the

¹Aided by a grant from the National Science Foundation, Washington, D.C.

²The author wishes to thank the following for having made this distributional work possible by making available the collections under their care: C. B. MacNeil, California Academy of Sciences, San Francisco; L. M. Martin, Los Angeles County Museum, Los Angeles; T. N. Freeman, Entomological Research Institute, Ottawa; F. Rindge, American Museum of Natural History, New York; Harry Clench, Carnegie Museum, Pittsburgh; W. S. Field and J. F. Gates Clark, U.S. National Museum, Washington, D.C.; and the Dept. of Entomology, Chicago Natural History Museum, Chicago, Illinois.

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"same species" as another, or a "subspecies" or "geographical race" of it, or should not be considered significantly different. These criteria will be more exhaustively dealt with in a later paper. For practicability, different criteria must be used at different times and in varying circumstances. The ultimate taxonomic designation is a product of weighing a great number of problems, some factors being known and others unknown, with the hope that the best result may be achieved. Another general rule underlies these studies; namely, that stability and uniformity are desirable in nomenclature, and that past taxonomic decisions should not be upset by hasty, poorly-thought-out changes. But the past should not remain immutable when the decision to change is demanded by sound study or experimental evidence. Implicit in all taxonomic studies is perhaps an amount of individual opinion, perhaps greater than in many more experimental sciences, but even this can be greatly reduced by conscious effort to separate fact from opinion. It is the belief of the author that all facts upon which decisions are based should be stated; these are the "data" which can be refuted. New decisions should be made then only upon presentations of new data. Taxonomy by "hunches" is to be avoided; decisions should be accompanied by evidences for and against any decisions made.

THE SPECIES OF *PIERIS*

There are five clearly defined species of *Pieris* in North America. Of these, only four were native prior to 1800. Besides these, there are two other groups of related populations which might be considered "species," or sibling species, and a large number of geographical variations within each of these species, many of which are distinctive enough to be called "geographical races" or subspecies. Division of the species into geographical races is not to be considered in this paper, with the exception of the two sibling species just mentioned.

Pieris rapae. This is one of two common European species of *Pieris*, the first immigrants of which appear to have been introduced into North America prior to 1860. Since that time, the species has spread over the whole of the United States and much of Canada and Mexico, wherever the natural vegetation has been at least partially replaced by European weeds, such as black mustard, or by cruciferous agriculture. This species has a wide range of habitat which is suitable for its existence, since it is found from the warm parts of the Gulf of Mexico nearly to the tundra of Canada, and from the Imperial Valley below sea level to high mountain meadows in the Sierra Nevada or the Rocky Mountains. The food plants utilized are a variety of cruciferous plants, among which are all varieties of cruciferous garden vegetables (cabbage, kohlrabi, kale, etc.) as well as many weedy plants such as mustards, radish, sisymbrium, etc. Some garden flowers such as nasturtium are also utilized. In view of the "weedy" nature of this species, no map is given to illustrate its distribution.

Pieris napi (Fig. 1). This species is found throughout northern Europe and Asia where there is in effect a continuity with the forms of North America across the Bering straits and the islands of the Bering Sea. This is the most northern of all of the species of *Pieris*, its range extending to the edge of the tundra or slightly beyond along its northern limits. The northern distributional limit from the Mackenzie River and east follows closely the northern limits of the tree line. The species exists along both the Pacific and Atlantic coast lines, but extends farther southward on the Pacific Coast than on the Atlantic Coast. The southern-most population on the immediate Pacific Coast line is at Lopez Canyon, San Luis Obispo County, California at about 35° north latitude. On the east coast at sea level, the most southern locality known is along the coast of New York and Connecticut opposite Long Island at 42° north latitude. However, at increasing elevations in the Appalachian Mountains southward, *P. napi* (or *P. virginienensis*) may be found as far south as the Great Smoky Mountains of Tennessee and North Carolina at about 35° north latitude. The southernmost extension of range of *Pieris napi* in the strict sense is in the vicinity of Connecticut and the Appalachians of Vermont, New Hampshire and Massachusetts. Westward, the range passes through the lower part of Ontario, Michigan, Wisconsin, Minnesota, Manitoba, Saskatchewan and Alberta, always staying north of the prairies. A fuller discussion of the relation of *Pieris napi* to *P. virginienensis* is to be had in a separate paper to follow this one.

Where the range of *P. napi* reaches the Rocky Mountains in central Alberta, the species extends clear to the Pacific coast and southward in the Rocky Mountains at increasing elevations to southern New Mexico and Arizona. The species appears to be absent in the drier ranges of the Great Basin and northward in the sagebrush country into south-central British Columbia. Elsewhere, it is widely distributed in the habitats that it prefers, these being damp wooded areas with partial shade, and temperatures not over seventy degrees Fahrenheit..

Of interest in the search for extensions of range are the following specific locations on the southern parts of the range of *Pieris napi*:

California: Coast — San Luis Obispo County, Lopez Canyon, December through May.

California: Western side Sierra Nevada, Merced County, Yosemite Valley, 3-4000 feet, April-May.

California: Eastern side Sierra Nevada, Placer County, 6-7000 feet, June.

Nevada: No records at present.

Arizona: Apache County, White Mountains, August; Gila County, "Globe" July.

New Mexico: Otero County, James Canyon, Cloudcroft, August, Carron 6, Mogollon, May, August.

Georgia: No records.



FIGURE 1. Map showing the North American distribution of *Pieris* (*Pieris*) *napi*.

South Carolina: No records.

North Carolina: Black Mountains, April.

Tennessee: Great Smoky National Park, Cherokee, April.

Some other points of interest in the distribution of this species are the following records:

Pribilof Islands, Alaska, July. Mouth of the Mackenzie River, North West Territories.

Great Bear Lake, N.W.T. Churchill, Manitoba (Hudson Bay).

James Bay, Hudson Bay, Quebec. Ramak, Labrador

Pieris napi is the only known butterfly to inhabit the Aleutian Islands, or the islands of the Bering Sea. This ability is probably correlated with its adaptation to existence at temperatures below 70°F, with low solar radiation and high humidity.

Pieris (Pontia) protodice (Fig. 2). This is the most widely distributed species of *Pieris* in North America. Some prefer to place this species, together with the following two species, in a separate genus *Pontia* for which there is much to recommend. To do so, however, would reduce the size of the genus *Pieris* beyond what would seem reasonable, and, therefore, to obviate this difficulty, and yet show phylogenetic relationship, *Pontia* would best be retained as a subgenus name.

Pieris protodice is best adapted to habitats with more sunshine than is required by *P. napi*. It also is enabled to survive in habitats much too warm for that species. However, cold does not seem to be a limiting factor as long as there is a short warm season and plenty of sunlight. These conditions, to some degree, pertain to the area occupied by the species. It apparently does not flourish in areas of continual hot temperatures as indicated by its absence in all fully tropical climates.

Pieris protodice differs from *P. napi* in its absence all along the immediate Pacific Coast from northern California through Alaska in keeping with its dislike for cool, cloudy areas. It is absent in the northern half of Alaska but eastward its distributional limits parallel those of the timbered area, as with *P. napi*. East of the Hudson Bay, however, *P. protodice* is absent north and east of Ottawa and New York State. The reasons for this event are baffling unless the present distribution of the species has been greatly disturbed by man in the eastern regions of North America as has been found true for *Colias eurytheme*. *Pieris protodice* prefers sunny, open fields as compared with *P. napi* which prefers partially shaded, damp areas. The cutting of the eastern deciduous forest to produce open fields for agriculture has aided both *Colias eurytheme* and *Pieris protodice* in extending their ranges and population density. It has probably also reduced the range and population density of *Pieris napi* since the habitats are conflicting. This probably accounts for the known diminution of *Pieris napi* in the region of Cambridge, Massachusetts where they were once exceedingly abundant, and now rare.



FIGURE 2. Map showing the North American distribution of *Pieris (Pontia) protodice*.

Pieris protodice is found throughout the southeast from Long Island to the southern part of Florida and around the Gulf of Mexico to Guatemala. It is very abundant in the highlands of Mexico but may be found nearly everywhere except in woods or forested areas. It is found from the southern tip of Lower California northwards, having a great preference for open areas. It is possible that its great abundance in southern California coastal areas is a recent event, correlated with the change of the natural perennial grasslands to annual European grasses, mixed with *Brassica nigra*, the black mustard. It reaches its greatest abundance, however, in the desert regions where conditions of cool nights, hot days, full sunlight and periodic extensive abundance of food plants (*Cleome*, *Brassica*, *Sisymbrium*, etc.) allow the species to swarm in clouds. In such areas, the population abundance is usually limited by the periodicity of available water.

In the mountain areas, the species is spread from the lowest valleys to the top of the highest mountains. The author has collected *Pieris protodice* at the top of Mt. Whitney, 14,500 feet elevation, the highest point in the United States south of Alaska, and in the bottom of Death Valley and Imperial Valley below sea level.

The relationship of *Pieris occidentalis* to *Pieris protodice* is here left in doubt, but for the purposes of the map (Fig. 2), they are considered forms of one species. This point will be considered in more detail in a future paper. There is no doubt that at higher elevations and cooler temperatures, populations exist which have a blacker, fuller pattern on their wings than populations which exist at lower elevations at higher temperatures. The preponderance of the evidence suggests that these differences are not hereditarily controlled, but that they are dependent entirely upon the environmental conditions. Within the species as a whole, as with *P. napi*, the darker individuals exist in the more northern latitudes at cooler temperatures than the lighter ones. However, this relationship must be reconciled with local factors. In Colorado, Brown (1957) has shown that *P. occidentalis* appears to form definite populations at high elevations whereas *P. protodice* forms populations at low elevations. F. Rindge, however, in a personal communication has found both in considerable number in the same valley in Utah. These points cannot be reconciled at the present time. *P. protodice* when exposed to low temperatures develops a color pattern (more extensive melanin) which is similar to, or identical with, *P. occidentalis*. They could very likely be genetically the same and if they are genetically the same, they are not deserving of a scientific or Latin name of significance nomenclatorially. This point has not been proved, however. In the case of geographical variations, such deviations are considered subspecific unless proved otherwise. In the case of altitudinal or seasonal differences, such as in *Pieris protodice* or *Colias eurytheme*, it is suggested that Latin names not be applied except to geographically isolated populations and then in a subspecies sense only.



FIGURE 3. Map showing the North American distribution of *Pieris (Pontia) sisymbrii*.

Pieris (Pontia) sisymbrii. (Fig. 3) The *Pontia* subgenus of the Pierids all prefer dry habitats with considerable sunshine exposure, unlike *Pieris napi* or even *Pieris rapae* which prefer or can survive in shade and high humidity. *Pieris sisymbrii* is one of these. Its habitats are always open, highly exposed, usually rocky places. It prefers cool temperatures but with high solar radiation. It lives in the spring time in the desert, as in the Mohave Desert where it flies at temperatures of highs not over 70° F, even though the temperatures later in the year will be over 100° F. It also lives in the mountains at elevations of over 10,000 feet in June and July. In the coastal area of California, its habitats are usually dry, rocky areas (serpentine, etc.) which are more dry and more exposed to solar radiation than its general position on the map would indicate.

Geographically (Fig. 3), the species exists throughout the mountainous areas of the west from the Yukon Territory to Mexico. It probably also exists in northern Mexico but there are no records. Outside of this area, there are a series of locations in the Northwest Territories from the Great Bear Lake southward past the Great Slave Lake to Lake Athabasca. Between these locations and the Rocky Mountains there are no locations known. This is probably due to lack of many suitable habitats. Collectors would do well to increase the known distribution of this species. It has a wide distribution but is characterized by the extreme isolated nature of them. Its habitats are narrowly restricted even on the desert and the adults have a short adult life, flying for only a few weeks during the year at any one place. The species aestivates and hibernates as a pupa which is very hard and impervious to water.

There is relatively little variation between the individuals in a population in this species, and also relatively little variation geographically between populations. Some variations have been described, however, and will be considered in a subsequent paper.

Pieris protodice is a species which is generally distributed and has many generations per year; it is therefore genetically and physiologically pliable as is necessary to meet these changed conditions. On the other hand, *Pieris sisymbrii* is greatly restricted to isolated habitats, and the adults fly only a short time; thus, the species genetically may be said to have developed a narrower range of tolerance through a narrower range of selective factors of the environment.

Pieris (Pontia) beckerii. (Fig. 4). Of all the species of North American *Pieris*, *P. beckerii* has the most restricted geographical range, extending from south-central British Columbia east of the Cascade Mountains southwards east of the Sierra Nevada into the deserts of southern California (Fig. 4). Its eastward limits coincide with the Rocky Mountain system in Montana, Wyoming and Colorado. The species does not extend into New Mexico so far as is known, unlike *Pieris sisymbrii*. The most southern-known limits are southwestern



FIGURE 4. Map showing the North American distribution of *Pieris (Pontia) beckerii*.

Colorado, central Arizona, and southern Nevada, except for California where the species may be found in the foothills of the mountain ranges especially on the desert side. However, the species has been found on the coastal side in the area of the Santa Susana Valley (Moorpark), San Fernando Valley, Santa Clara River Valley and on the immediate coast from San Diego and southwards.

Pieris beckerii exists at elevations of sea level at the coast and some parts of the desert to 9000 feet in the mountain valleys. It has always been found in areas that are relatively dry or desert-like with high solar radiation. Its distributional range coincides almost perfectly with that of the semi-arid brushlands extending from the rain-shadow valleys of central British Columbia, throughout the Great Basin and inter-mountain valleys of the Rocky Mountains. The factors that limit its distribution in southern Arizona, New Mexico and northern Mexico are unknown. Perhaps there is a lack of proper food plant. The distribution of the species in southern California south of the Great Basin is correlated closely with the distribution of *Isomeris arborea*, its preferred food plant. It seems likely, however, that some other plant may also satisfy for this purpose. There is little doubt that intensive searching for additional populations of *Pieris beckerii* in the range of *Isomeris* will extend the distribution some considerable distance, especially in the south Coast Ranges of California, the foothills of the Sierra Nevada and southward in Baja California.

Unlike *Pieris sisymbrii* which has a single short generation per year, in southern California, *Pieris beckerii* has a succession of generations with the bulk of the adult flight being correlated with the time of the winter rains. However, in the mountainous regions north of the Mohave Desert, the species has only one known generation, in the early summer.

There is little geographical, local population, or seasonal variation in *Pieris beckerii*. However, some races have been described and will be considered in a later paper.

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